

A NEW LABYRINTHODONT AMPHIBIAN FROM THE CARBONIFEROUS OF SCOTLAND

by T. R. SMITHSON

ABSTRACT. Cranial remains of a labyrinthodont amphibian *Doragnathus woodi* gen. et sp. nov., from localities in the Viséan and Namurian of the Scottish Carboniferous, are described. The structure of the lower jaw resembles that of the earliest known Amphibia, but its dentition is unusual, comprising large numbers of strongly incurved, closely spaced marginal teeth together with a row of small needle-like coronoid teeth. The relationships of *Doragnathus* are discussed. A specimen of *Doragnathus* from Pitcorthie represents the earliest recorded labyrinthodont in the British Carboniferous.

THE Scottish Midland Valley is one of the few areas in the world from which fossil Amphibia have been found in Carboniferous sediments older than those equivalent in age to the British Coal Measures (Westphalian and Stephanian). Thirteen pre-Coal Measure genera have so far been described from a total of eleven Scottish localities. Most discoveries were made in the latter half of the last century, but recently a diverse amphibian fauna was discovered in a bone bed at the Dora Opencast Site, near Cowdenbeath, Fife (Andrews, Browne, Panchen, and Wood 1977; Smithson, in press). With the exception of an almost complete skeleton of *Crassigyrynus scoticus* (Panchen, in press) the Cowdenbeath fauna is represented by dissociated skeletal elements of at least six amphibian genera. The most common of these is a hitherto undescribed labyrinthodont represented by a large number of incomplete jaw specimens. The new form has also been found at Pitcorthie and Niddrie (Smithson, in press) and recently by Mr. Stanley Wood and the author on the island of Inchkeith, in the Firth of Forth.

Labyrinthodonts are rare components of the Scottish Lower Carboniferous amphibian assemblage, and until recently they had been recorded at only three of the eight Lower Carboniferous localities. The recognition that a jaw specimen from Pitcorthie in the collection of the Royal Scottish Museum was that of a labyrinthodont and not, as had previously been thought, a lepospondyl, and the discovery of similar material on the Island of Inchkeith, has improved this position. Although these new specimens are incomplete and poorly preserved, material from the Upper Carboniferous deposits at Cowdenbeath and Niddrie allows a description of a number of aspects of the cranial anatomy of the new labyrinthodont to be given.

The fossiliferous deposits on the island of Inchkeith and at Pitcorthie occur in strata of Viséan age. The middle of the exposed sequence on Inchkeith is thought to be equivalent to the horizon of the Burdiehouse Limestone (Davis 1936). The fossiliferous sediments at Pitcorthie almost certainly occur within the Anstruther Beds (Forsyth and Chisholm 1973). These lie below the Cuniger Rock Marine Band which has been placed, on palynological evidence, well below the Burdiehouse Limestone (Neves *et al.* 1973). Thus the amphibian remains from Pitcorthie are older than those from the Burdiehouse Limestone, and the labyrinthodont remains are the earliest recorded in the British Carboniferous.

Where necessary material was prepared with a dental mallet and industrial 'Airbrasive' unit, and a solution of 'Perspex' dissolved in chloroform was used to repair breaks in specimens.

The following abbreviations are used for the institutions owning the material: NUZ, Department of Zoology (University of Newcastle upon Tyne); RSM, Department of Geology (Royal Scottish Museum).

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA

Subclass LABYRINTHODONTIA

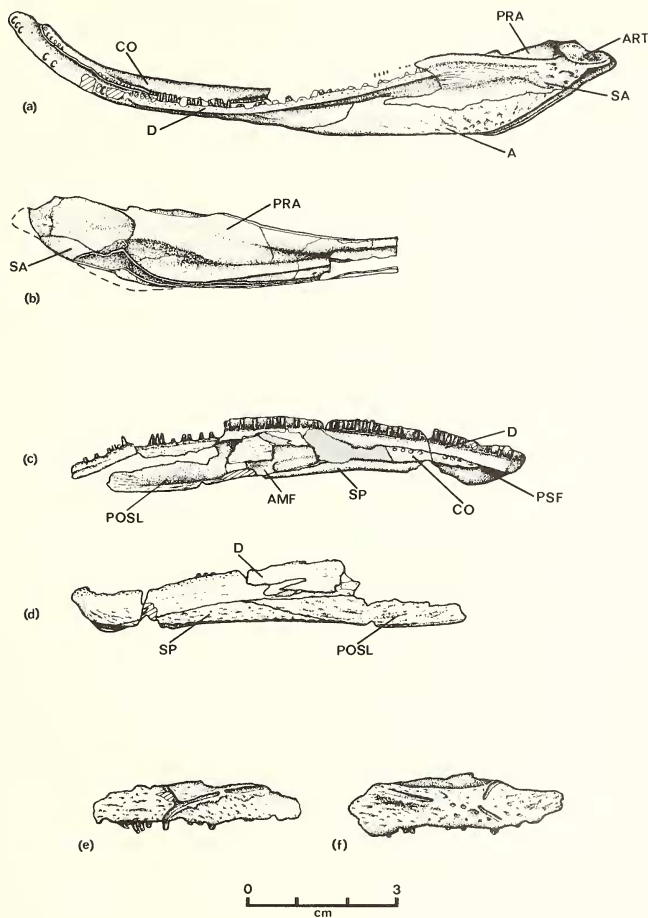
Order and Family Undesignated

Doragnathus gen. nov.*Type species. Doragnathus woodi* gen. et sp. nov.*Etymology.* The name refers to the large number of jaw specimens from the Dora Opencast Site.*Diagnosis.* Labyrinthodont amphibian with a long, shallow lower jaw which terminates with a distinct retroarticular process; small Meckelian fenestra at the mesial exposure of the splenial/post splenial suture; dentary with room for more than eighty closely spaced, strongly incurred teeth, labyrinthine unfolding of enamel found only below the margin of the gums; a row of slim needle-like replaceable teeth on the coronoid series.*Doragnathus woodi* gen. et sp. nov.

Text-figures 1-3

Etymology. The animal is named after Mr. Stanley Wood, who discovered the bonebed at the Dora Opencast Site which has yielded the majority of the material attributed to *Doragnathus*.*Diagnosis.* As for genus.*Holotype.* NUZ 77.5.26 incomplete left ramus of lower jaw.*Type horizon and locality.* Localized seatrock, beneath a coal seam below the Lochgelly Blackband Ionstone, upper part of the Limestone Coal Group (Namurian A, Upper Carboniferous), Dora Opencast Site, Cowdenbeath, Fife, Scotland.*Distribution.* Scottish Midland Valley (Lothian and Fife regions).*Range.* Middle Calciferous Sandstone Measures (Anstruther Beds) to Upper Limestone Group (South Parrot Coal Shale). C₂S₁? zone of Viséan stage (Lower Carboniferous) to E₂ zone of Namurian A (Upper Carboniferous).*Description.* The description of *Doragnathus* is based on the most complete specimens in the collections of the Royal Scottish Museum and the University of Newcastle upon Tyne. All have suffered *post-mortem* compression and only RSM GY 1898.107.51 is preserved in any degree of completeness (text-fig. 1a, b). A complete list of attributed material is deposited in the Department of Geology, Royal Scottish Museum.*Lower jaw.* In its over-all construction the lower jaw is similar to that of early labyrinthodonts, e.g. *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1952) and *Metaxygnathus* (Campbell and Bell 1977). Each ramus is relatively shallow throughout its length, tapering slightly towards the symphysis in lateral view. In dorsal view each ramus curves gently towards the midline and, when articulated, the two jaws describe a distinct U. The majority of specimens are from animals with lower jaws approximately 12 cm long. A number of specimens, notably RSM GY 1975.5.3, have been found at Cowdenbeath which are considerably larger; the estimated lower jaw length of the largest of these is approximately 30 cm. The smallest recorded specimen, RSM GY 1881.43.24 from Pitcorrhie, has a lower jaw approximately 6 cm long. (All measurements included in this description have been taken from specimens approximately 12 cm in length.)

A well-defined mandibular lateral line canal follows the ventral edge of the jaw ramus. At regular intervals it is partially or completely bridged with bone and appears as a series of ovoid pits approximately 1.5 mm long along their antero-posterior axis and approximately 1 mm wide. The adductor fossa is preserved in RSM GY 1898.107.51 and RSM GY 1975.5.3. It is a steep-sided cavity, approximately 2.8 cm long, walled laterally by the surangular and mesially by the prearticular. The dorsal surface of the surangular is slightly convex but is not developed into the high surangular crest of anthracosaurs and certain temnospondyls. Anteriorly the fossa tapers and is bounded by the posterior coronoid at the level of the tooth row. Half-way along the floor of the fossa in RSM GY 1898.107.51 is a small raised rugosity which probably acted as a point of



TEXT-FIG. 1. *Doragnathus woodi* lower jaw and premaxillary, natural size. (a) lateral, (b) mesial view of lower jaw RSM GY 1898.107.51; (c) mesial, (d) lateral view of holotype NUZ 77.8.28; (e) external view right premaxillary NUZ 77.5.26; (f) external view left premaxillary NUS 78.1.26. Damaged bone surfaces, hatched; matrix, regular stipple. A, angular; AMF, anterior Meckelian fenestra; ART, articular; CO, coronoid; D, dentary; POSL, postsplenial; PRA, prearticular; PSF, postsymphysial foramen; SA, surangular; SP, splenial.

attachment for a mass of the adductor mandibulae musculature. In the tunnel formed between the inner and outer walls of the ramus the cavity extends as the Meckelian space, which may have been partially occupied by Meckel's cartilage (Nilsson 1944).

The Meckelian fenestrae are small and restricted to the ventral margin of the mesial surface of the jaw. They are preserved only in the holotype (text-fig. 1c). The most anterior fenestra perforates the jaw at the junction of the splenial and the postsplenial bones. A second, smaller fenestra may be present approximately 1 cm behind the first. Unfortunately, this region is badly damaged and interpretation is difficult. The posterior Meckelian fenestra normally found at the junction of the postsplenial and angular is absent.

The mesial surface of the symphyseal region is comparatively smooth and exhibits none of the roughened areas for ligamentous attachment normally expected. The apparent absence of strong points of ligament attachment suggests that the symphysis was comparatively weak and a certain degree of movement of the jaw rami relative to one another was possible. Immediately behind the symphysis the dentary is roughly triangular in section, one side forming the lateral surface of the jaw, a second the mesial wall, and the third a tooth-bearing shelf. Directly below the tooth-bearing shelf, the mesial wall is pierced by the postsymphyseal foramen. Posterior to this, the infradentary bones are incorporated into the mesial and lateral surfaces of the jaw and to the mesial edge of the tooth-bearing shelf are attached the coronoids. The greatest exposure of the dentary is in the lateral wall. Anteriorly it is approximately 5 mm deep, gently deepening posteriorly to reach its maximum depth towards the end of the tooth row. Extending along its dorsal edge is a finely ornamented border. Below this the dentary is almost smooth: only behind the symphysis is the dentary ornamented with irregular ridges and grooves. In dorsal view the tooth-bearing shelf extends from the symphysis to terminate immediately in front of the adductor fossa. Throughout its length the shelf maintains an almost constant width. It has room for more than eighty closely spaced, strongly incurved teeth. Details of the dentition are discussed separately.

The coronoids extend from behind the symphysis to the adductor fossa and form an almost horizontal roof to the Meckelian space. Small replaceable needle-like teeth extend along the lateral edges of the coronoids and form a single row of teeth lying parallel to those on the dentary. The series widens posteriorly eventually forming the anterior border of the adductor fossa. Unlike some later labyrinthodonts, the posterior coronoid is not incorporated into the lateral wall of the fossa. It was not possible to trace the sutures between the individual coronoids.

The Meckelian space is floored by the two splenials and the angular. The (pre-)splenial contacts the dentary behind the symphysis. Laterally the suture between the two bones is long and straight and runs parallel with the ventral jaw margin.

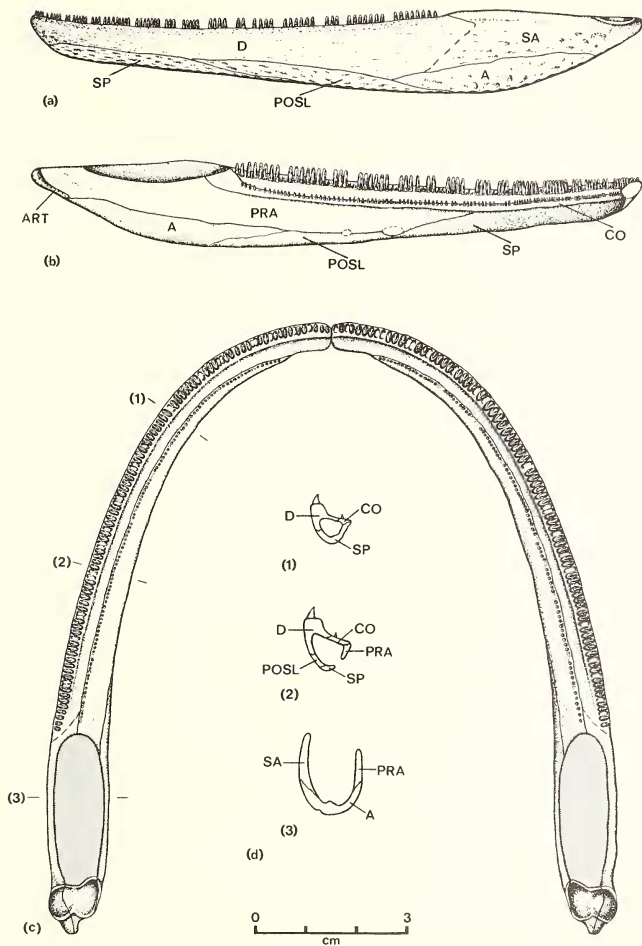
Posteriorly the splenial contacts the postsplenial along an oblique suture which passes under the ventral edge of the jaw. Both elements are ornamented with the irregular ridges and grooves found on the dentary. In mesial exposure it contacts the anterior coronoid under the mesial border of the coronoid shelf. Along the length of the suture the angle between the two bones is approximately ninety degrees. Posteriorly the dorsal edge of the splenial gently tapers away from the coronoid shelf to form a broad suture with the prearticular which contacts the postsplenial at the jaw margin. Lying at the junction of the three elements is the anterior Meckelian fossa. The postsplenial is a narrow strip of bone which, in lateral exposure, contacts the dentary along most of its length and posteriorly sutures with the angular. It contacts the prearticular along a broad suture mesially and posteriorly continues to contact the angular. Between the postsplenial and prearticular a second small Meckelian fenestra may be present lying approximately 1 cm behind the first.

The posterior part of the lateral wall of the ramus is formed by the angular and surangular. Both are ornamented with a system of ridges and pits which are less well defined than those on the two splenials. The angular wraps around the posterior edge of the ramus to present a relatively narrow exposure on the mesial surface where it has a long straight suture with the prearticular.

Behind the tooth row, the lateral dorsal margin of the jaw is formed by the gently convex rim of the surangular. Posteriorly it sheathes the articular, extending behind the glenoid to form the lateral wall of a short retroarticular process. Passing down the posterior edge of the process is the surangular articular suture. In dorsal view, the rim of the surangular which sheathes the articular is thickened and incorporated into the glenoid fossa. The suture between the surangular and dentary could not be traced.

The mesial wall of the adductor fossa is formed principally by the prearticular, a long narrow element which extends forward to fill much of the inner surface of the jaw. Posteriorly it sheathes the articular and is incorporated into the glenoid, but unlike the surangular does not form part of the retroarticular process. It sutures with the angular and splenial bones ventrally and its dorsal edge contacts the posterior coronoid to form the anterior margin of the adductor fossa.

The remaining element in the lower jaw is the articular which represents the only ossification of Meckel's cartilage. It is embraced on its lateral and mesial surfaces by the surangular and prearticular respectively, but



TEXT-FIG. 2. *Doragnathus woodi* lower jaw. Composite restoration, natural size. (a) lateral, (b) mesial, (c) dorsal view, (d) transverse sections of jaw at positions indicated in (c). Abbreviations as in text-fig. 1.

only on its mesial surface is it exposed where it extends posteriorly to form the internal surface of the retroarticular process. The shape of the glenoid fossa, when viewed dorsally, resembles a distorted figure of eight. This is clearly seen in RSM GY 1975.5.3. The articular surface is divided into two subcircular depressions by a ridge oriented along the anterior posterior axis of the jaw. The mesial depression extends slightly further forward than that on the lateral surface of the fossa. Both are bounded anteriorly by a well-defined precondyloid process. The postcondyloid process is not clearly defined since the posterior margin of the fossa is incorporated into the retroarticular process. The foramen for the chorda tympani (mandibular) branch of the seventh nerve, which in most Amphibia pierces the lower jaw just below the glenoid fossa, could not be traced.

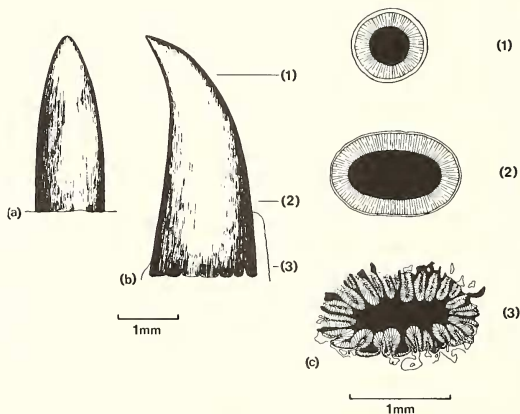
Premaxilla. A number of isolated, partially complete, premaxillae containing marginal teeth of the type described from the lower jaw of *Doragnathus* have been found at Cowdenbeath. All are thought to be from skulls with a lower jaw length of approximately 12 cm. In antero-lateral view the premaxilla is a narrow elongate element ornamented with irregular ridges and grooves as found on the splenials of the lower jaw. In ventral aspect it is gently curved and mirrors the shape of the anterior region of the mandible. There is room for more than twenty-five teeth. The premaxillary margin of the choana is not preserved on any specimen.

The supraorbital lateral line canal passes across the exterior surface of the premaxilla. It extends over the posterior dorsal edge onto the nasal and along the antero-lateral edge to join the second half of the supraorbital canal on the opposite premaxilla. The canal is manifest in a variety of ways. In NUZ 77.5.26 it appears as an open groove which is bridged over with bone at one point only. In NUZ 78.2.26, however, it is bridged over much of its length and is visible as an irregular series of pits (text-fig. 1e, f). Only where it runs over onto the nasal and opposite premaxillary does it appear in an open groove.

In palatal aspect, the premaxilla extends posteriorly as a broad shelf of bone to suture with the vomers. The presence of a palatal fenestra is improbable.

Maxilla. An incomplete maxilla has been found at Pitcorthie (RSM GY 1881.43.24). Apart from showing that the maxillary teeth are of the type found on the dentary and premaxilla, it yields little information.

Dentition. The marginal teeth in the upper and lower jaws of *Doragnathus* are identical. They are of uniform size along most of the tooth row becoming smaller towards its posterior end. There is no parasymphysial tusk on the lower jaw and no peaking along the dentary or maxillary. In lateral view the teeth are bullet-shaped and in posterior aspect strongly incurved (text-fig. 3b). Their bases are twice as wide as long and narrow towards the apex of the tooth, becoming almost circular in section just below the tip.



TEXT-FIG. 3. *Doragnathus woodi* teeth. (a) lateral, (b) posterior view of marginal tooth $\times 12$; (c) transverse sections through tooth as positions indicated in (b), $\times 20$.

Labyrinthine infolding of the enamel is only found at the base of the teeth below the margin of the gums. In section they show the characteristic infolding of the external primary dentine, but whereas in many osteolepiform crossopterygians and most labyrinthodonts the infoldings meander and some cases are branched (Schultze 1969), those of *Doragnathus* appear as straight, nonconvolute unbranched folds (text-fig. 3c). The majority of teeth from which histological sections have been taken in fish and in other labyrinthodonts have been the large tusk teeth on the palate and the coronoids. However, the marginal dentition of most crossopterygians comprises teeth considerably smaller than the tusk teeth and these exhibit simple folding, e.g. *Megalichthys* (Schultze 1969, p. 94), of a type very similar to that found in *Doragnathus*. The tortuous infolding often taken to typify labyrinthodont teeth is undoubtedly a size-related phenomenon, a fact clearly demonstrated by Bystrov and Efremov (1940, p. 46).

The teeth are arranged in the jaw as a series of 'clusters and gaps'. Normally approximately seven teeth are grouped together as a cluster and separated from a similar cluster by one or two replacement pits. However, groups of smaller than seven occur particularly in the middle of the tooth row and the over-all pattern of tooth replacement is unclear.

The coronoid dentition comprises a single row of small, replaceable, needle-like teeth which lie parallel to the marginal row. The palatal dentition is unknown.

DISCUSSION

The paucity of complete or partially complete specimens of *Doragnathus* prevents a satisfactory analysis of its relationships, but certain features of its lower jaw allow a number of points to be considered. The over-all structure of the jaw resembles that of the earliest known Amphibia. It differs from those of rhipidistian fishes in a number of respects, notably the largest teeth in the jaw are found in the dentary, the coronoid teeth are small and there are no coronoid fangs. The prearticular fails to reach the symphysis and the mesial surface of the jaw is perforated anteriorly by at least one Meckelian fenestra.

The position of *Doragnathus* within the Amphibia seems clear. Its average skull size (represented by specimens with lower jaws 12 cm long) is larger than that found in the majority of non-labyrinthodont amphibians, and the largest specimens are considerably larger than any known 'lepospondyl'. The infolded internal structure of the marginal teeth suggest its inclusion within the Labyrinthodontia, but infolded teeth have been found in the microsaure *Trihecaton* (Vaughn 1972), and it is possible that infolding is primarily a function of tooth size (Thomson and Bossy 1970). However, one additional feature which suggests affinity with the labyrinthodonts is the presence of an anterior Meckelian fenestra. No non-labyrinthodont is known in which the mesial exposure of the splenial/postsplenial suture is perforated.

The position of *Doragnathus* within the Labyrinthodontia is less certain. In most respects its lower jaw is primitive and resembles that of *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1952), and *Metaxygnathus* (Campbell and Bell 1977). Each has a retroarticular process and an extensive prearticular which forms much of the mesial wall of the jaw. A single row of teeth is present on the coronoids lying parallel to the marginal row on the dentary. However, the parasymphysial tusks present in *Ichthyostega* (Campbell and Bell 1977) are absent in *Metaxygnathus* and *Doragnathus*. Parasymphysial tusks are present in the majority of early labyrinthodonts, e.g. colosteids (Panchen 1975), loxommatids (*sensu* Beaumont 1977), *Crassigyrinus* (as '*Macromerium*' Panchen 1973; see Panchen, in press) and *Caerorhachis* (Holmes and Carroll 1977), and their absence in *Metaxygnathus* and *Doragnathus* may be significant. However, in forms in which the dentition is irregular and the teeth numerous and of uniform size and shape, tusks are usually lost completely, e.g. the loxammatoid *Spathicephalus* (Tilley 1971). This principle may also apply to *Doragnathus*, and the absence of parasymphysial tusks need not necessarily indicate close relationship. In addition a number of differences in the structure of the lower jaw suggest that the two genera are not closely related, notably the absence in *Metaxygnathus* of an anterior Meckelian fenestra, the shallow lateral extent of the dentary, and the high elevation of the articular above the tooth row.

Both *Doragnathus* and *Spathicephalus* occur at Cowdenbeath (Smithson, in press) but are easily distinguished by differences in their dentition. The marginal teeth of *Spathicephalus* are chisel-shaped

in lateral view and are not incurved (Smithson in press, text-fig. 2) and coronoid teeth are restricted to the anterior coronoid (E. H. Beaumont (*née* Tilley) pers. comm.). Whilst differences in the dentition of the two forms indicate a clear generic distinction, the possibility of close relationship cannot be ruled out. Unfortunately the lower jaw of *Spathicephalus* is inadequately known and little direct comparison can be made to clarify the problem.

In a recent review of the Namurian amphibian fauna I tentatively suggested that *Doragnathus* be included within the Trimerorhachoidea (Smithson, in press). This suggestion now seems untenable. Although the lower jaws bear superficial resemblance, the presence of a posterior Meckelian fenestra in trimerorhachids and the posterior extension of the posterior coronoid, either incorporated into the surangular crest (e.g. in *Trimerorhachis* Williston 1914) or forming a distinct coronoid process (e.g. *Dvinosaurus* Bystrow 1938), almost certainly precludes close relationship.

It is clear that the position of *Doragnathus* within the Labyrinthodontia is uncertain. Those features which it shares with other forms are almost certainly primitive for labyrinthodonts as a whole and, until more complete material is available, the taxonomic position of *Doragnathus* will remain obscure. Only in the arrangement of the dentition, notably the uniform structure and large number of marginal teeth, does the lower jaw of *Doragnathus* differ significantly from those of other early labyrinthodonts.

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